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GLIDING GROWTH AND THE BARS OF SANIO

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INTRODUCTION

By gliding growth is meant the independent elongation or enlargement of cells in the growing zone which occurs, as some maintain, during differentiation and radial growth. The bars of Sanio are said to consist of cellulose and pectic materials in the form of bars or imperfect tubes which extend through two or more cells arising from the same initial in a direction at right angles to the plane of division. These bars have been studied chiefly as they occur in the xylem and phloem of trees, but have also been shown to occur in the more superficial cells of woody plants, where they extend parallel to the surface instead of as radii, as is the case with those arising in the cambial zone of trees.

The bars arising in the cambium have been brought into discussions to refute the contention that certain cells on arising from the cambium undergo elongation during differentiation, as well as in studies on the phylogenetic relationship of some Coniferae. In investigations into the nature and activity of the cambial sheath the bars have also been used. It seems, therefore, that gliding growth and the bars of Sanio have been of much interest to botanists during many years. The present discussion aims to contribute some concrete evidence on the subject of gliding growth and at the same time to make brief mention of the related literature.

SOME HISTORICAL ASPECTS

Most of the earlier investigators who incidentally studied this matter in connection with the differentiation of the cells from the cambium infer that gliding growth occurs, but their inferences were usually not based on sufficient tangible data.¹

¹ Trécul, A. Origine et developement des fibres ligneuses. *Ann. Sc. Nat. Bot.*, 3. Ser. 19: 63-74. 1853. Hartig, Th. Ueber die Entwicklung des Jahrringes der Holzpflanzen. *Bot. Zeit.* 11: 553-60; 69-79. 1853. Velten, W. Ueber die Ent-

Krabbe² made a special study of the subject of gliding growth and found that it is typical of the cells differentiating to form the characteristic cellular elements of fibrovascular bundles in both monocotyledons and dicotyledons. He found that in the case of certain monocots practically the entire xylem of the secondary fibrovascular bundles arises from single vertical rows of cells which grow many times their original length gliding past each other, thus producing a bundle instead of a row of cells. He holds, however, that cell elongation occurs only while the cells adjoining are still growing. The same was maintained by him regarding the special enlargement of certain cells to form vessels; *i. e.*, gliding growth in the transverse direction. Mischke,³ as well as Nathansohn⁴ later published some inferential corroborative evidence supporting Krabbe's findings. A more recent substantial contribution to the subject of gliding growth is by Jost.⁵ In his study of the behavior of the cambium in crotches and where branches arise from a trunk, he has concluded that although continued increase in thickness of the two components at such branching points necessitates a reduction in area of the cambial mantle or sheath, no cambium is actually eliminated. He therefore assumed that the cells of the cambium glide between each other as the area to be covered becomes smaller and that the cytoplasmic connections obtaining between the cambial cells are re-established at the conclusion of the gliding growth. He also thinks that primary rays of stems are divided and the parts displaced laterally to form many narrow rays by the gliding of the cambial cells in such a way as to break up the very broad primary rays.

wicklung des Cambium, und N. J. C. Müller's Ideen über diesen Gegenstand. Bot. Zeit. 33: 809-14; 825-29; 841-45. 1875. Russow, E. Über die Perforation der Zellwand und den Zusammenhang der Protoplastmakörper benachbarter Zellen. Sitzungsber. Naturforscher. Gesellsch. Univ. Dorpat. 6: 562-82. 1884. Schenck, H. Ueber die Auskleidung der Intercellulargänge. Ber. Deut. Bot. Gesellsch. 3: 217-24. 1885. Sanio, K. Jahrb. Wiss. Bot. 9: 123; Bot. Zeit. 21: 107-108. 1863. Haberlandt, G. Die Entwicklungsgeschichte des mechanischen Gewebesystems, p. 44, 1879.

² Krabbe, G. Das gleitende Wachsthum bei der Gewebebildung der Gefäßpflanzen, pp. vii + 100, pl. 7, 1886, Berlin.

³ Mischke, K. Beobachtungen über das Dickenwachstum der Coniferen. Bot. Centralbl. 44: 39-43; 65-71; 97-102; 137-42; 169-75. 1890.

⁴ Nathansohn, A. Beiträge zur Kenntniss des Wachsthum's der trachealen Elemente. Jahrb. Wiss. Bot. 32: 671-86. 1898.

⁵ Jost, L. Ueber einige Eigenthümlichkeiten des Cambiums der Bäume. Bot. Zeit. 59: 1-24. 1901. -

A paper by Klinken⁶ has just appeared, in which the subject of gliding growth is discussed from various angles. The study was based on serial and other radial sections of *Taxus* taken through the cambial region, and including both xylem and phloem. Longitudinal gliding growth was found to occur in the xylem but not in the phloem. The cambium cells were found to undergo unlimited gliding growth or independent elongation. They were found to undergo transverse divisions after attaining certain lengths. Some of his published figures also indicate that some of the xylem cells coming into contact with medullary rays are often bent and curve somewhat to one side.

Neeff⁷ recently contributed some interesting observations on gliding growth. He noticed that in the wood the ends of some cells were often compressed between others where resistance to elongation appears to have been too great. A figure is given showing a case where two cells are being forced apart by an intruder; the two halves of a pit are forced apart. See figure 6, which is copied from Neeff. Similar occurrences were also found in the phloem, as shown in the same figure noted above. He also found cases in which pits, corresponding to those that had been displaced by gliding growth, had apparently been formed in the walls of new neighbors. On the other hand, instances were also noted in which the pit connections existing between cells prevented gliding growth or retarded it to such an extent as to cause a decided compression or puckering of the growing cells.

The fact that the bars of Sanio occurring in the most closely related cells of a radial row always form a continuous and unbroken bar is regarded as indicative that gliding growth is of very minor importance or is wholly lacking. According to Raatz⁸ the running of bars through only one or a few cells is indicative that the meristematic cell in which such bars originated underwent only a limited number of divisions before being forced out of the cambial zone by the progressive differentiation of the cells in the cambium sheath. The long bars that extend through one or more season's growth, on the other hand, are said to have arisen in a meristematic cell in the most active part

⁶ Klinken, J. Über das gleitende Wachstum der Initialen im Kambium der Koniferen und den Markstrahlverlauf in ihrer sekundären Rinde. *Bibliotheca Botanica* 19: Heft 84, pp. 41, 1914.

⁷ Neeff, F. Über Zellumlagerung. Ein Beitrag zur experimentellen Anatomie. *Zeitschr. Bot.* 6: 465-547. 1914.

⁸ Raatz, Wilh. Die Stäbbildungen im sekundären Holzkörper der Bäume und die Initialentheorie. *Jahrb. Wiss. Bot.* 23: 567-636. 1892.

of the cambial sheath and which therefore continued to give rise to new xylem and phloem cells during a considerable period before its last derivative arrived at a position in the cambium where it was forced to become differentiated into a mature cell and cease further division. Such an argument not only tends to show that cells through which these bars extend have not glided on each other, since they arose from each other by division, but also indicates, as Raatz and later Nordhausen,⁹ Schoute,¹⁰ and Müller¹¹ maintained, that Sanio's simple hypothesis on the nature and method of origin of cells from the cambium does not cover the facts of cambial division as it occurs in our trees. Incidentally it may also be mentioned that since Raatz and others found these bars occurring in numerous and widely separated species of trees, and Petri¹² has more recently shown them to occur in the cultivated varieties of the grape when affected by a disease known as "courte noue," they seem to have very little of phylogenetic significance in the conifers as maintained by Gerry¹³ and others. Groom and Rushton¹⁴ have recently also contributed to the question of the bars or rims of Sanio.

GLIDING GROWTH IN APPLE (*Pyrus malus* L.)

While studying the development of the initial stages of crown-rot of apple trees in cross sections it was frequently noticed that the more or less regular radial rows of wood cells arising from corresponding rows in the cambial zone are separated by cells in their angles. The diameter of the intruding cells nearest the cambium was usually very slight and increased as the distance from the cambial zone increased. These intercalated cells were suspected of being some that

⁹ Nordhausen, M. Zur Kenntniss der Wachstumsvorgänge im Verdickungsringe der Dikotylen. Beiträge Wiss. Bot. 2: 356-400. 1898.

¹⁰ Schoute, J. C. Über Zellteilungsvorgänge im Cambium. Verhandl. K. Akad. Wetensch. Amsterdam 9: Sect. 2, pp. 66, 1902.

¹¹ Müller, C. Ueber die Balken in den Holzelementen der Coniferen. Ber. Deut. Bot. Gesellsch. 8: (17)-(46), 1890.

¹² Petri, L. Ricerche sulle cause dei deperimenti delle viti in Sicilia. 1. Contributo allo studio dell' azione degli abbassamenti di temperatura sulle viti in rapporto all' arricciamiento. Mem. R. Staz. Pat. Veg., 1912, pp. 212, Roma.

¹³ Gerry, E. The Distribution of the "Bars of Sanio" in the Coniferales. Ann. Bot. 24: 119-23. 1910.

¹⁴ Groom, P., and Rushton, W. Structure of the Wood of East Indian Species of Pinus. Jour. Linn. Soc. Bot. 41: 457-90. 1913.

had entered the level of the section from one side or the other by growing in length and penetrating between the ends of the neighboring cells. Such an idea seemed plausible because of the fact that the intruded cells nearest the cambium are small and no corresponding radial rows could be found in the cambial zone from which they could have arisen. The absence of a corresponding row from the phloem also showed that such cells present in the xylem could not have arisen from an eliminated cambial row.

In case wood cells undergo longitudinal growth after arising from the cambium, it appeared likely that in occasional sections one ought to find unmated pits in cells that had been forced apart, for, as has been well established, many of the pits are derived from the cambium cells by division and must therefore be present on cell walls before gliding growth has been completed.

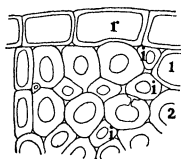


FIG. 1. *Cross Section of Apple Wood*, showing cells nearest cambium at left and a monoseriatic medullary ray along the upper edge of figure. *r*, medullary ray. *1* and *2*, regular rows of xylem cells derived from the cambium at this level. *i*, cells intruding between the regular rows at their angles.

As a matter of fact, several such instances were found, one of which is reproduced in figure 1. The fourth cell from the left in the lower radial row (2) of this figure shows an unmated pit, although the corresponding cell of the next row (1), that evidently arose from a cambium cell at this level, shows no corresponding pit. Along the upper edge of the figure is a medullary ray and on the left are the last wood cells of two radial rows that had been differentiated from the cambium. Between the two radial rows, arising from the cambium at the left, are seen what appear to be intruding cells (i) mentioned above. These intruders seem to have forced their way between their neighbors at the angles, at points where one usually finds angular intercellular spaces.

Longitudinal radial sections, however, furnished the most direct and therefore the most conclusive proof yet published to show that gliding growth occurs. A careful examination of many slides showed that the ends of wood fibers are often compressed and diverted at medullary rays, as had been found by Neeff. In some cases not only the ends of the wood cells in contact with medullary rays were flattened and enlarged, but the ray cells encountered were also compressed. In other instances the ends of the wood-cells were found diverted to

one side into a direction more or less parallel to that of the rays, as may be seen in figure 2. Much variation was evident in the length of that portion of cells that was diverted from the direction of the other wood cells toward that of the rays; in one instance the diverted portion was found to measure $15.7\ \mu$ in length (figure 3). In several

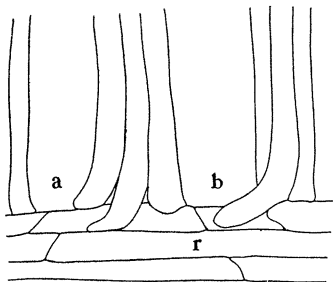


FIG. 2. *Longitudinal, Radial Section of Apple Wood.* *a* and *b*, large vessels. *r*, medullary ray.

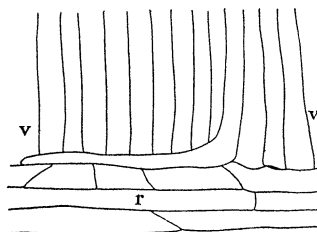


FIG. 3. *Longitudinal Section of Apple Wood,* showing one cell that has undergone considerable independent elongation. *v*, large vessels. *r*, medullary ray.

instances pits were found on the convex side of such bent wood cells in positions where the cell was not in contact with any other. Such cases were found in the bent groups outlined in figures 2 and 5.

The diverted tips seem to have grown in various directions. In figures 3 and 5 the growth was along the ray toward the bark, which

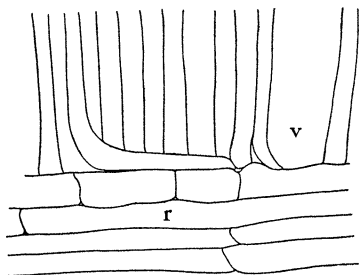


FIG. 4. *Section of Apple Wood,* showing various degrees of elongation of xylem cells. *v*, large vessel. *r*, medullary ray.

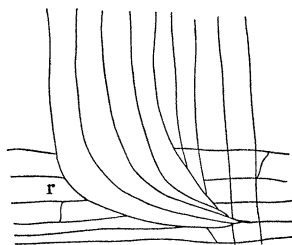


FIG. 5. *Section of Apple Wood,* showing a group of xylem cells diverted at end by encountering a medullary ray, *r*.

appeared to indicate that the gliding was toward the less lignified cells; but in the cases shown in figures 2 and 4 the matter is different. In the instance figured in 2, the ends of the cells curved toward the

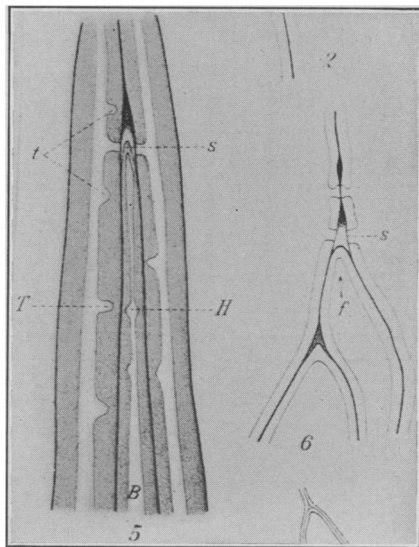


FIG. 6. *Longitudinal Sections, showing Gliding Growth.* *B*, elongating phloem cell intruding between two neighbors and forcing them apart, as shown at the pits. *f*, elongating xylem cell intruding between and forcing apart two other cells, as shown at the pit *s*. (Figures copied from Neeff's article, *Über Zellumlagerung* Zeit. für Bot. 6: 465-547. 1914.)

large vessels (*a*) and (*b*), while in 4 the curvature was away from the bark. It is seen to be in the direction of a vessel (*v*) that is rather remote from the starting point of the long glide.

GENERAL DISCUSSION

It appears to be an established fact that the Bars of Sanio run continuously through certain radial groups of cells in the wood and bark; and that such groups probably arose from the divisions undergone by a meristematic cell and its progeny subsequent to the origin of the bar, and before the last daughter cell of the group is forced from the cambial zone and becomes differentiated into mature tissue. The fact that the bars present in the different cells of such a

group form an unbroken bar at maturity is not conclusive proof that the cells of such groups could necessarily not have undergone gliding growth; for it seems likely that the differential gliding growth takes place chiefly at the ends of the cells. The evidence recently given by Klinken, Neeff, and that found in apple appear to add sufficient direct proof to that formerly published to show beyond a doubt that gliding growth occurs among the differentiating wood cells of trees. The fact that pits in wood are often found to open into intercellular spaces instead of meeting corresponding pits in neighboring cells also shows that they are not closed even when cellular displacements have deprived them of their former relations or functions. On the other hand, the fact that unpaired pits are not of more frequent occurrence seems to argue that Jost's assumption to the effect that displaced pits induce the formation of corresponding pits on contact with the walls of other cells, is probably often the case, except perhaps in instances where the unpitted walls encountered are too old. Neeff's observations also support such a view.

The tissue fusions resulting from budding and grafting also give support to the notion that pit connections that have been ruptured during gliding growth are subsequently resumed with the new neighbors on the completion of the process. However, it seems that actual contact with other tissues is not always necessary to induce the formation of pits, for many cases were found in proliferating tissues of apple and pear stems in which the proliferated cells were not in contact with other cells and yet contained pits. Vöchting¹⁵ has made similar observations in *Brassica*.

Pits are often penetrated by very fine cytoplasmic threads that Strasburger¹⁶ called Plasmodesmen. Such connecting threads have recently also been found to exist between the components of so-called graft hybrids.¹⁷ Since cytoplasmic connections occur very generally between plant cells associated in tissues, it appears that they must frequently be ruptured in places where gliding growth occurs. That being the case, it seems unavoidable that thin cytoplasmic smears

¹⁵ Vöchting, H. Untersuchungen zur experimentellen Anatomie und Pathologie des Pflanzenkörpers. Tübingen, 1908, pp. vii + 318, pls. 20.

¹⁶ Strasburger, E. Ueber Plasmaverbindungen Pflanzlicher Zellen. *Jahrb. Wiss. Bot.* 36: 493-610. 1901.

¹⁷ Hume, M. On the Presence of Connecting Threads in Graft Hybrids. *New Phytologist* 6: 216-221. 1913.

would result between the cells of such tissue, and that some intercellular spaces might be lined with thin films of such cytoplasm. According to Kny's¹⁸ observations, published about ten years ago, intercellular cytoplasm is present in seeds of *Lupinus*. A little later,¹⁹ however, he claims to have been in error in his first observations, in that the cytoplasm noted is said to have been carried to the intercellular spaces by the sectioning knife.

¹⁸ Kny, L. Studien über intercellulares Protoplasma. Ber. Deut. Bot. Gesellsch. 22: 29-35; 347-55. 1904.

¹⁹ ——— 23: 96-98. 1905.